MORPHOGENESIS, VASCULARIZATION AND PHYLOGENY IN ANGIOSPERMS[1, 2]

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ABSTRACT. Evidence is reviewed to support the hypothesis that vascular strands in the angiosperm flower which some botanists have regarded as "vestigial" can be understood better if they are regarded as the result of irregularities in development, which provides no indication with respect to the alternatives of phylogenetic reduction vs. amplification. Nevertheless, the concept of the conservatism of vascular anatomy is supported by the probability that genes acting late in development can more easily give rise to mutations that can become incorporated into a harmonious genotype than can genes that act early in development. Examples from the development of achenes in various genera of the family Compositae show that size of mature achene is not necessarily correlated with complexity of vascular anatomy, and that this anatomy may reflect the particular course of development, particularly the time when procambial initials are differentiated. In this family, genera that are generally regarded as more closely related to each other tend to have more similar developmental patterns than those that are more distantly related.

Ever since the 19th-century research of Celakovsky (1896), botanists have asked the question: "Is the arrangement of vascular bundles in the organs of higher plants a more reliable guide than outward form to homology and the direction of evolution?" Until very recently, the usual answer has been affirmative (Eames, 1931, 1961; Puri, 1951, 1952; Melville, 1962), al-

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though botanists have differed widely with respect to interpretations of anatomical structure. In particular, single vascular bundles that appear to have no function have been designated as "vestigial." They have been interpreted as vestiges of organs that are no longer formed, and therefore as indicating widespread, predominant trends of reduction. Furthermore, the concept of "fusion" has been adopted to interpret situations in which two related species or genera differ with respect to the number of parallel bundles found in an organ. If a form has two parallel bundles in a particular position, it is regarded as more generalized or primitive than a related form that has only one bundle in that position.

During the last decade, botanists have become increasingly skeptical of such notions. An extreme form of this skepticism has been expressed by Carlquist (1969). After an extensive review of the entire problem, he reaches the following conclusion (p. 334): "Anatomy of flowers can be studied meaningfully only in relation to adaptations for particular modes of pollination, dispersal and allied functions."

In my opinion, neither the rigid interpretations of Eames, Puri, Melville and their followers nor the complete skepticism of Carlquist are justified. Later in this article, examples are given to show that when comparing even such similar and certainly homologous structures as the achenes of different Compositae, one finds many exceptions to a supposed correlation between organ size and complexity of vascularization. On the other hand, several examples exist in the literature to show that supposed "vestigial bundles" can be associated with either increase or decrease in numbers of parts. One of the clearest of these was presented long ago by Murbeck (1914). In two species belonging to the family Rosaceae, *Comarum palustre* and *Alchemilla vulgaris* (sens. lat.), he found rare deviations from the normal or modal number of calyx lobes, in both an upward and a downward direction. In *Alchemilla*, for instance (Fig. 1), the normal number of lobes is four, but occasional flowers have three lobes and others have five. Most important, however, is the fact that among 3-lobed as well as among 4-lobed calyces are examples in which one of the lobes is larger, and may have a double-pointed apex, as well as extra vascular bundles. According to the classical interpretation, such 3-lobed calyces result from a trend of reduction via "fusion," and the extra bundles found in the larger lobe are "vestigial." If, however, this interpretation
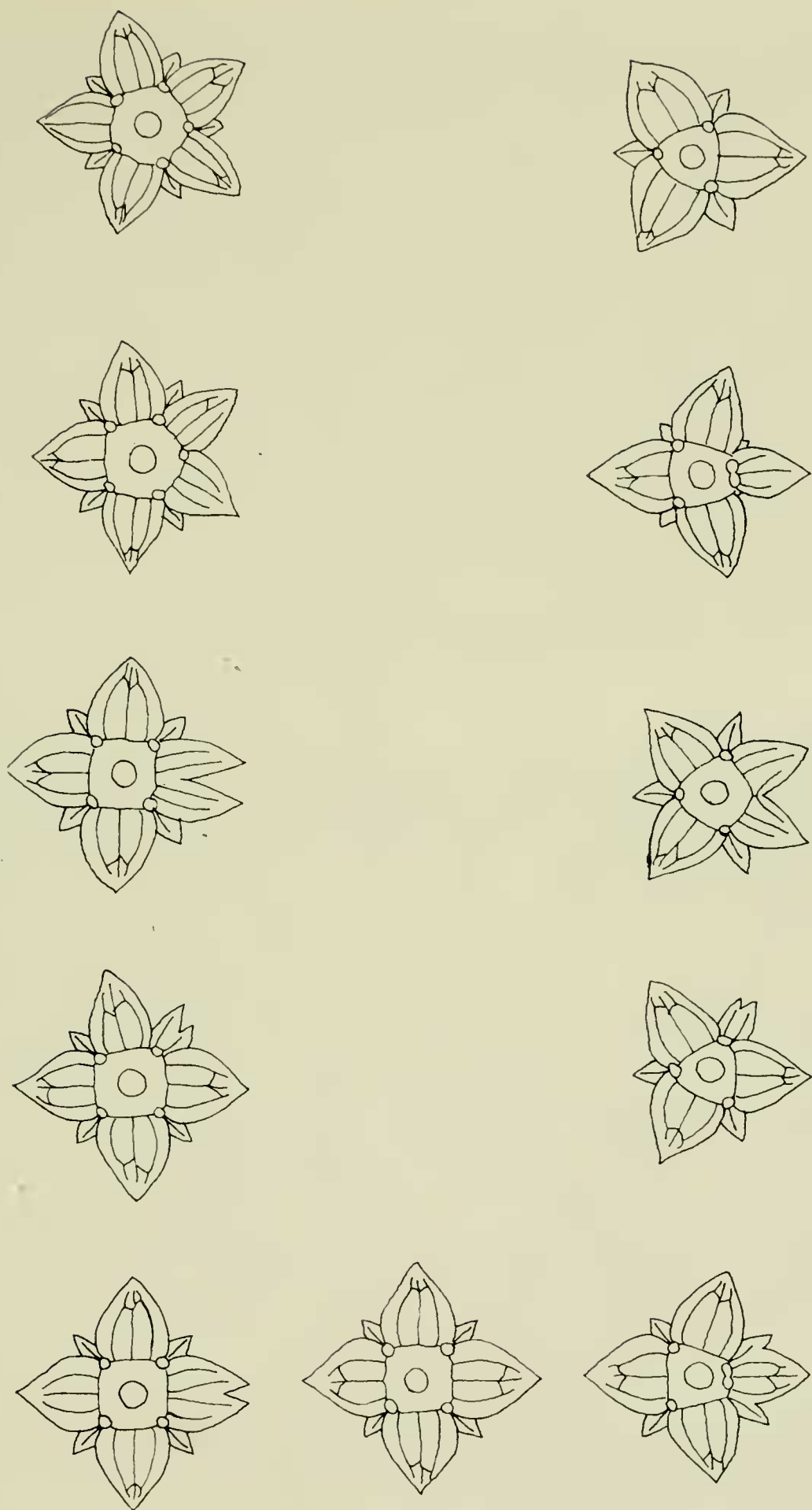
Figure 1. Calyces of individuals of *Alchemilla vulgaris,* showing devia-tions from the normal 4-merous condition in the direction of both decrease and increase in lobe number, as well as intermediate situations with ab-normal lobe number and structure. From Murbeck, 1914.

is to be consistent, the larger lobes of the aberrant 4-lobed calyces would have to be interpreted in the same way, and the conclusion would have to be reached that the basic number of calyx lobes in *Alchemilla vulgaris* is five rather than four. Such an interpretation is contradicted by the fact that 4-merous calyces are found throughout the genus *Alchemilla*, except for rare aberrant individuals like those described by Murbeck. In *Comarum palustre*, similar aberrant calyces have five lobes, one of which is larger than the others and contains extra vascular bundles. If one held strictly to the concept of reduction and vestigial bundles, one would have to interpret these calyces as indicating that the calyx of *Comarum* was originally hexamerous. Since hexamerous calyces are almost completely lacking, not only in the family Rosaceae but also in the entire order Rosales, such an interpretation is absurd.

A Morphogenetic Intrepretation of "Vestigial Bundles"

These examples are best interpreted by discarding entirely the concept of reduction and vestigial bundles, as well as any other phylogenetic concept, and regarding them entirely in the light of developmental genetics. The aberrant calyces found by Murbeck are comparable to the aberrant corollas described by Huether (1968) in *Linanthus androsaceus*, and shown by him to represent unusual gene combinations that render the plant more susceptible than normal individuals to producing aberrant phenotypes, or phenodeviants, as a result of normal environmental fluctuations during development. Deviations from the normal or modal condition can occur in either direction. Using a developmental approach, they can be explained on the basis of a formula that I suggested a few years ago (Stebbins, 1967). The number of similar organs or parts that are produced in a particular whorl can be represented by the quotient $A^n + \dfrac{a^m}{a^i}$, where A^n is the final number of parts, a^m is the total number of meristematic cells that are capable of producing an A-type part, and a^i is the number of meristematic cell initials needed to produce a single A-type part.

Applying this formula to Murbeck's examples, one could suggest that in the normal development of the calyx of *Alchemilla*, the relation of a^m to a^i is on the order of 20 to 5, so that $A^n = 4$.

In the extreme aberrants, a^i remains the same, but a^n has become respectively 15 and 25. On the other hand, 3-lobed calyces of which one lobe is larger and has extra bundles would result from values such as $a^m = 17$ and $a^i = 5$, so that $A^n = 3.4$. Similarly, abnormal 4-lobed calyces would represent the quotient $A^n = 4.4$, resulting from values of $A^m = 22$ and $a^i = 5$.

Morphogenetic evidence with respect to "vestigial" bundles in the androecium of various species belonging to the order Malvales has been obtained by van Heel (1966). He showed that in several instances vascular bundles, which in the mature flower were not associated with any recognizable structure, nevertheless appeared in a position where small stamen primordia could be recognized in early stages of development. These primordia later became enveloped by the growth of the surrounding tissue, presumably produced by persistent intercalary meristems. These examples could be regarded either as terminal stages of a reduction series, or intermediate stages of a trend toward amplification.

The most convincing evidence regarding the morphogenetic significance of vascularization comes, however, from experiments in which the conditions under which vascular tissue appears have been determined, or have been altered in specific ways. Only two such experiments are known to me. One of them, by Wetmore and Rier (1963), showed that vascular tissue arises in callus tissue at positions that are at regular distances from each other, and that their distributional pattern can be altered as a result of relatively slight alterations in the nutritive medium. Consequently, the appearance of a bundle in an unexpected position requires only a slight shift in the distribution of nutritional factors or in the balance of hormonal interactions within the developing system.

In the other experiment, Torrey (1955, 1957) altered experimentally the number of protoxylem points in a pea root. He found that when 0.5 mm of the distal portion of the root, containing only cells that are not visibly differentiated, was isolated and cultured *in vitro*, the great majority of cultures produced roots having the normal triarch condition. About 2 percent of the cultures, however, which were tips of relatively small size, produced at first diarch roots, which later reverted to the triarch condition.

If to the culture he added indole acetic acid at a concentration of 10^{-5} molar, he obtained a greater proliferation of the cells

from which vascular tissues are differentiated. As a result, he converted the triarch to the hexarch condition, and found that the latter condition persisted indefinitely. The number of protoxylem points could, therefore, be increased or decreased, depending upon the amount of meristem present when procambial differentiation took place.

These two experiments suggest that much can be learned about the processes that affect the pattern of vascularization by various kinds of experimental approach. This is a field of morphogenesis that has not yet been well developed but that promises eventually to provide a bridge over which visible changes in vascular anatomy can be related to specific alterations of the genotype, as they affect developmental processes.

Vestigial Characters in Plants and Animals

The results just reviewed suggest that with respect to any group of similar structures, such as parts of a perianth, stamens in an androecium, or "carpels" in a gynoecium, evolutionary change can involve either increase or decrease in number, and that the anatomical features associated with either trend are similar to each other. Vascular anatomy cannot tell us whether or not the ancestors of a particular form had more or fewer sepals, petals, stamens, or carpels.

The belief of plant anatomists that this is possible rests, in my opinion, on a mistaken analogy with the genuine vestigial structures found in animals. These latter, such as the gill slits of the vertebrate embryo and the vermiform appendix, have a complex and distinctive developmental pattern. The so-called "vestigial bundles," on the other hand, are identical in structure with the bundles that are unquestionably functional. Furthermore, the procambial cells that form the xylem and phloem of these bundles are probably differentiated from meristematic cells during a single mitotic cycle (Olson et al., 1969). More important, the epigenetic sequence responsible for the formation of these bundles is an exact repetition of a course of events that occurs in many other parts of the plant; only the position where it occurs is distinctive.

A Developmental Hypothesis That Favors Conservatism of Vascular Anatomy

The concept of vestigial bundles is part of a broader concept

that views vascular anatomy as more conservative than external
morphology. This concept has been rejected by Carlquist (1969)
as an "insufficient and fallacious framework on which most
phylogenetic interpretations of floral anatomy still rest." He
nevertheless concedes that degree of union between vascular
bundles can be "conservative." Is there any logic to this ac-
ceptance of a part of the doctrine of conservatism, after most
of it has been rejected?

I believe that botanists must examine the problem from the
viewpoint of developmental genetics and morphogenesis, since
this brings us closer to the basic nature of evolutionary changes.
When we do this, we can recognize and emphasize the fact that
the procambial initials from which vascular bundles arise become
differentiated from the ground meristem at a very early stage
of the development of primordia. Consequently, alterations of
vascular pattern require changes in the time of action of genes
that normally act very early in development. Alterations in the
action of genes that normally act at later developmental stages
can produce changes in size or form without altering the pattern
of vascularization.

Is there any logical reason for assuming that genes which
produce their effects at early stages of development are less likely
to play a role in evolutionary change than genes which affect
later stages? A positive answer to this question is the genetic
basis for recognizing Von Baer's principle of embryonic similar-
ity, which was used by Darwin (1872) as embryological evi-
dence for evolution, and has been applied more recently to
animal development by De Beer (1951), and to plants by the
present author (Stebbins, 1950). The reasoning is as follows.
Adult characteristics are assumed to be the products of epi-
genetic sequences of gene action in development, so that later
processes depend in part upon the nature of gene products pro-
duced at earlier developmental stages. Moreover, the action of
most genes is pleiotropic in the sense that their primary products
may have many secondary effects. The earlier is this primary
action, the greater is the amount of pleiotropy that is possible,
and the more widespread are the secondary effects of genes.
Hence mutations of genes affecting early stages are more likely
to produce profound alterations of development, and hence to
upset the entire developmental system, than are mutations of
late-acting genes. The milder alterations produced by these
latter mutations are more likely to adjust the individual in a

harmonious fashion to new selective pressures than are the more drastic effects produced by mutations of genes that act early in development. Hence, adaptive alterations of morphology are brought about more often by late-acting genes than by those acting early in development. In other words, genes acting early in development tend to be conservative with respect to the establishment of their mutations in populations. Among such genes are those that affect the differentiation of procambial strands.

Relationships Between Organ Size and Amount of Vascularization

In the remainder of this contribution, I would like to apply the theoretical concept just developed to two situations. The first is the relationship between organ size and amount of vascularization. If vascularization is related only to adaptation and physiological function, as Carlquist has assumed, then large organs should always have a proportionately greater amount of vascularization than homologous, smaller ones. On the other hand, if preferential establishment of late-acting gene changes is a significant factor, then the relationship between size and vascularization would have a historical or evolutionary component.

Among homologous organs having approximately the same size, but different patterns of vascularization, one might postulate that the one having the more complex pattern resembles most closely the most primitive organ of the group in question, while the simpler pattern has been derived by a process of reduction that affected early stages of development, followed by a reversal of evolutionary direction, in which increase in size was accomplished by establishment of genes acting late in development. Similarly, in comparisons between homologous organs of very different sizes, but having similar, relatively simple patterns of vascularization, one might postulate that the smaller organ more nearly resembles a reduced, ancestral form, and the larger one has been derived via secondary enlargement.
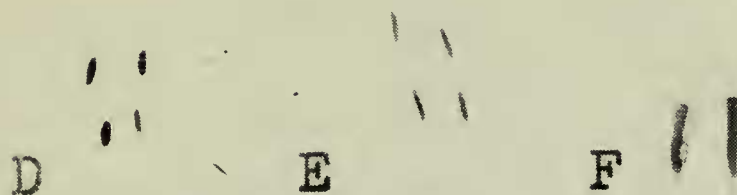
Ovary and Achene Development in the Family Compositae

A good object for testing these hypotheses is the ovary and achene in the family Compositae. In different genera of this

Figure 2.   Mature achenes of various species of Compositae of which the development is recorded in Tables 1 and 2. A, *Helianthus annuus,* wild form from east of Davis, Calif. B, *Helianthus annuus,* cultivated variety from Department of Agronomy, University of California, Davis. C, *Wyethia glabra,* from Cache Creek Canyon, Yolo County, Calif. D, *Senecio cruentus,* cult. var. *"stellata"* (smaller heads) . E, *Senecio vulgaris,* from campus, University of California, Davis. F, *Microseris nutans,* from Wright's Lake, Eldorado County, Calif. G, *Tragopogon porrifolius,* from Locke, Sacramento County, Calif. H, *Stephanomeria exigua* ssp. *coronaria,* from Antioch, Calif. I, *Microseris douglasii,* from south of Dixon, Solano County, Calif.

family, an enormous range of size exists between mature achenes having a length of 1.4 mm to achenes 20 times as long, and many-fold greater in bulk (Fig. 2). With respect to anatomy, the most complex patterns consist of 26 to 28 parallel bundles traversing the ovary and achene (Stebbins, 1940), while in the simplest ones, only two bundles are present (Stebbins, 1937). The poor correlation between size and complexity of vascularization is shown in Figure 2, which illustrates the mature achenes of ten forms belonging to this family. In three of these (A–C), the ovary and achene are traversed by 12 to 28 parallel vascular strands, while in the remaining three (G–J) only five are present. In the first group, achene length ranges from 2.92 mm to 13.65 mm; in the second, from 1.4 mm to 5 mm; and in the third, from 3.8 mm to 28.5 mm. I admit that the largest example of the latter group, *Tragopogon porrifolius*, was chosen to represent an extreme example of large size associated with a relatively simple vascular pattern, so that one cannot conclude from this tiny sample that an inverse correlation exists between achene size and amount of vascularization. Nevertheless, the lack of a significant positive correlation in the family as a whole seems to me highly probable on the basis of my acquaintance with a large number of genera.

In order to discover more about the relationships between vascularization and developmental patterns, I have compared the ovaries of these species at four stages of development: (1) the smallest size at which procambial strands can be recognized; (2) the first appearance of xylem tracheids; (3) anthesis; and (4) mature achenes. Since the Composite achene increases far more in length than in width, mean length of the ovary at each of these stages is a reliable indicator of overall size. The stages were determined both from sectioned material and from whole mounts cleared according to the schedule of Herr (1971) and observed under Nomarski interference-contrast optics.

Preliminary results of this study are shown in Tables 1 and 2. Table 1 gives the mean lengths of the ovary and achene at four different stages: differentiation of procambium; first differentiation of xylem strands, anthesis, and seed maturity. The final column of this table gives the mean number of vascular strands in the ovary at anthesis. Table 2 presents the mean percentage growth increment for each interval between the stages listed in Table 1. To obtain these values, the difference between the length at a later stage and at the next earlier stage,

Table 1. Lengths of ovaries and achenes of some species and varieties of Compositae at selected stages.

Species or variety	Procambial differen- tiation (P)	Xylem differen- tiation (X)	Anthesis (A)	Maturity (M)	Xylem strands at anthesis
Wyethia glabra	0.253mm	0.631mm	11.25mm	13.65mm	12–17
Helianthus bolanderi ssp. exilis	0.198	0.291	2.01	2.92	19–21
Helianthus annuus wild (near Davis, Cal.)	0.251	0.38	1.596	5.52	18–24
Helianthus annuus cultivated	0.208	0.442	9.90	13.65	26–28
Senecio cruentus cult. small heads	0.234	0.732	0.868	1.43	10
Senecio cruentus cult. large heads	0.228	0.61	1.41	1.66	10
Senecio vulgaris	0.186	0.772	1.135	2.35	10
Microseris nutans	0.294	0.997	1.366	5.04	10
Microseris douglasii	0.194	0.999	1.67	4.96	5
Stephanomeria exigua	0.205	0.524	1.449	3.86	5
Tragopogon porrifolius	0.242	0.934	1.912	28.5	5

Table 2. Proportional growth increments at successive stages of ovaries of Compositae. Symbols explained in Table 1, and in text.

| Species or variety	$\dfrac{X\text{-}P}{P}$	$\dfrac{A\text{-}X}{X}$	$\dfrac{M\text{-}A}{A}$
Wyethia glabra	1.49	16.8	0.23
Helianthus bolanderi ssp. exilis	0.47	5.91	0.45
Helianthus annuus wild	0.51	3.20	2.46
Helianthus annuus cultivated	1.12	21.40	0.38
Senécio cruentus cult. small heads	2.12	0.17	0.65
Senecio cruentus cult. large heads	1.70	1.31	0.18
Senecio vulgaris	3.10	0.47	1.07
Microseris nutans	2.39	0.37	2.69
Microseris douglassi	4.15	0.67	1.97
Stephanomeria exigua	1.56	1.77	1.66
Tragopogon porrifolius	2.85	1.05	13.91
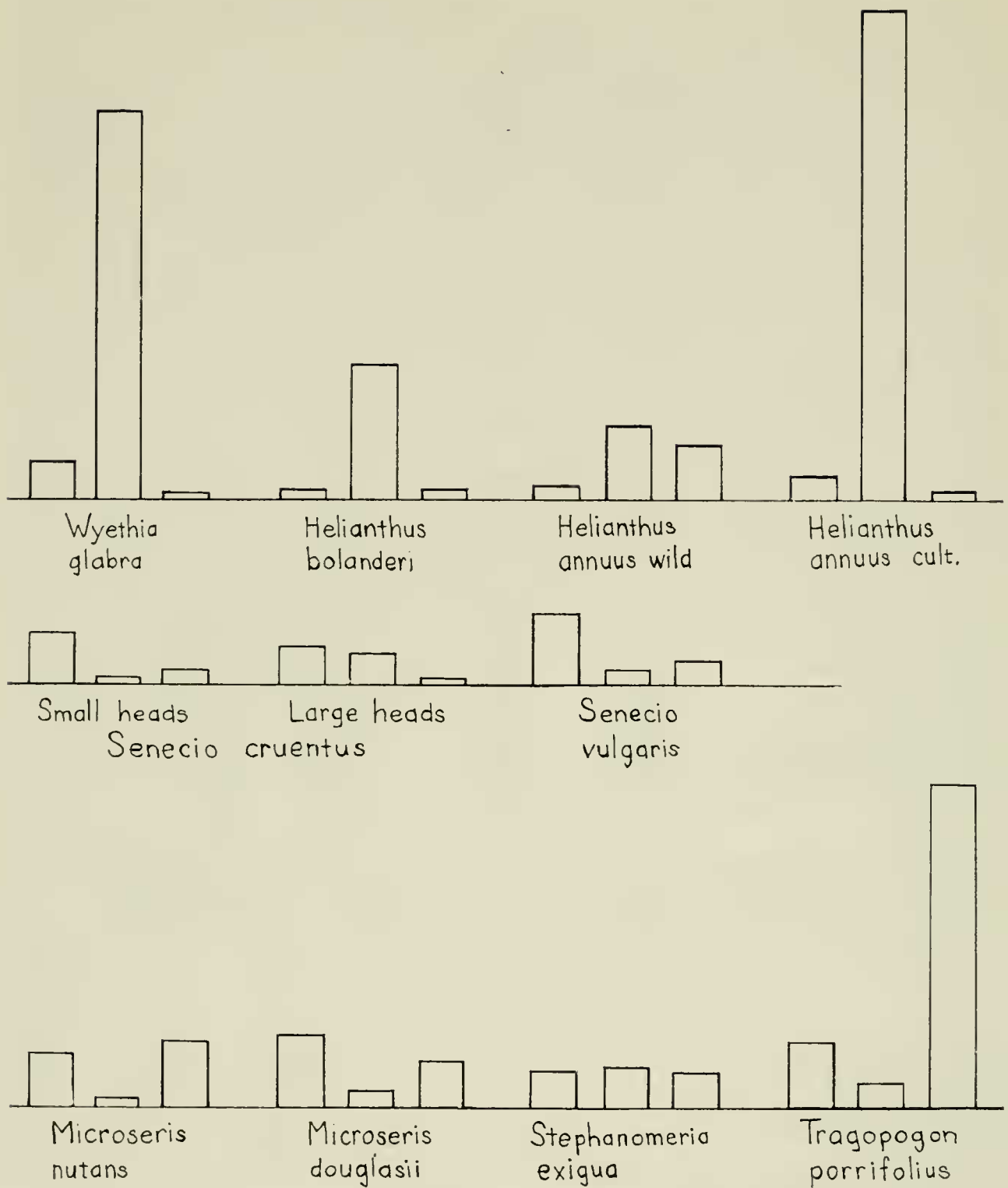
Figure 3. Chart showing diagramatically the growth increments of ovaries of Compositae, as recorded in Table 2.

i.e., the amount of growth during the interval, is divided by the length at the earlier stage. In this way, growth during each interval between stages is expressed in proportion to the amount of tissue or "meristematic capital" present at the beginning of the interval under study. In Figure 3, the same results are presented graphically.

These figures show that the amount of growth which takes place before the vascular pattern is laid down by procambial differentiation is only a small percentage of the total growth of the organ. Moreover, this percentage varies greatly from one species to another. The size of the primordium at the time of procambial differentiation is similar in all of the species studied, ranging from 186 micra in *Senecio vulgaris* to 294 micra in *Microseris nutans*. This range is far less than the extreme differences in size between mature achenes, so that the percentage of growth in length that takes place before procambial differentiation ranges from high figures to 14 to 16 percent in *Senecio cruentus* to the extremely low figure of 0.9 percent in *Tragopogon porrifolius*.

Two obvious conclusions can be made from these results. First, developmental patterns differ widely from one species to another of this family, and may even differ between varieties of the same species, as in *Helianthus annuus* and *Senecio cruentus*. Second, each of the tribes represented possesses a characteristic series of patterns that are different from those found in other tribes. In the Heliantheae, for instance, the greatest percentage increase in size occurs between procambial differentiation and xylem differentiation. The Cichorieae are more variable in this respect, but show a greater tendency than other tribes toward growth between anthesis and achene maturity.

A further conclusion can be drawn by comparisons between members of the same tribe. In both of the comparisons between cultivated varieties of the same species: wild vs. cultivated *Helianthus annuus* and the two cultivated varieties of *Senecio cruentus*, the greatest difference exists with respect to size increase between xylem differentiation and anthesis, a stage during which few or no mitotic divisions are taking place. In *Senecio*, this is also the stage at which the greatest difference exists between the two species studied: *S. vulgaris* and *S. cruentus*. In the Heliantheae, the two wild species of *Helianthus* differ most from *Wyethia glabra* with respect to the increase at this stage,

but the greatest difference between *H. annuus* and *H. Bolanderi* is with respect to the stage between anthesis and seed maturity. In the Cichorieae, the most divergent species, *Tragopogon porrifolius*, differs most from the others with respect to this last stage.

These results support, in general, the hypothesis that later developmental stages are more easily modified at the level of varieties and species than are early stages. In all of the varietal and species comparisons, except for the species of *Microseris*, stages after xylem differentiation differ more than do earlier stages. Furthermore, the size of the primordium at the time of procambial differentiation is strikingly similar among all of the forms studied, at least in comparison to the much greater differences between their mature achenes. Finally, with respect to the two examples of artificial selection for increased size, genetic changes affecting later stages were established in preference to those affecting earlier stages.

The comparison between the two species of *Microseris* provides a significant exception to the above generalization. The annual species, *M. Douglasii*, differs from the perennial *M. nutans* with respect to the smaller size of the ovary primordium at the stage of procambial differentiation, and the proportionally greater amount of growth that takes place between this stage and that of xylem differentiation. This suggests that *M. Douglasii* arose from its perennial ancestor, which certainly was not *M. nutans*, but may have been a species having a similar developmental pattern, via reduction in the size of the ovary primordium, accompanied or followed by compensatory growth at later stages. This reduction, which affected an early developmental stage, may have been responsible for the reduction from ten ovarian bundles, which is characteristic of *M. nutans* and other perennial species of *Microseris*, to five bundles, as found in most or all of the annual species, including *M. Douglasii*.

This small and admittedly inadequate sample supports, as far as it goes, the hypothesis that large achenes having simple vascular patterns are derived by secondary enlargement from smaller ones having similar vascularization. With respect to the hypothesis that simplification of vascular pattern takes place via a "bottleneck" of reduction that affects early developmental stages, followed by secondary enlargement, the present evidence is inconclusive. I hope, however, to obtain an answer to this question when the study is complete.

A Basis For Differentiating Between Primary and Secondary Union of Parts

The second kind of situation that I would like to discuss concerns the validity of vascular patterns as evidence for the phylogenetic origin of "fusions" and "adnations" between parts. This topic has been much discussed in connection with the origin of the inferior ovary, or epigyny (Douglas, 1957; Kaplan, 1967). The extreme skepticism of Carlquist (1969) with respect to such evidence has been challenged by Kaplan (1971), who in my opinion has successfully answered many of Carlquist's criticisms. At any rate, since diverse vascular patterns are found in various genera having epigynous gynoecia, is association with other very different morphological characteristics as well as affinities to various groups having perigynous or hypogynous gynoecia, this evidence indicates strongly that the epigynous condition has been evolved many times independently in different orders of plants, by various evolutionary pathways.

In my discussion, however, I should like to focus attention on the androecium. The "fusion" of stamens into bundles or a tubular staminal column that includes the entire androecium is a familiar feature in several plant families, particularly the Malvaceae, Sterculiaceae, Hypericaceae (Guttiferae), Myrtaceae, and some genera of Dilleniaceae. This "fusion" is generally regarded as secondary (Eames, 1961), and in most instances this conclusion is well justified. Developmentally, it is most often brought about by a suppression of differentiation with respect to stamen filaments. Instead of separate intercalary meristems that produce the growth of each individual filament, a common meristem elevates some or all of the anther primordia on a single column, tube or sheath (van Heel, 1966).

Recent developmental studies, however, suggest that not all "fusions" between stamens are of this secondary kind. In *Paeonia* (Hiepko, 1965) and *Hypericum* (Leins, 1964; Robson, 1972) careful analyses of the development of floral primordia have shown that stamen bundles, not individual anther primordia, fit into the phyllotactic sequence that is followed by the other floral parts. Furthermore, anther primordia arise not from the undifferentiated meristem of the reproductive axis, but from distinct primordia of stamen bundles. Their differentiation precedes the activity of the intercalary filament meristem, which in

Paeonia and *Hypericum* elevates each stamen upon a separate filament.

The anatomical condition that follows this developmental pattern is that of a common "trunk" vascular strand for each cluster of stamens that are differentiated from the same bundle primordium. The vascular strands that supply individual stamens diverge from the "trunk" strand, not directly from the floral axis.

Examination of the vascular anatomy of the mature androecium in a number of relatively primitive angiosperms, such as *Degeneria* (Swamy, 1949), *Hibbertia* (Wilson, 1965), and certain Annonaceae (*Cananga, Goniothalmus,* unpublished observations of the present author), has revealed the same kind of bundle pattern in them. In most instances, this pattern is not accompanied by an obvious clustering of the stamens in the flower as viewed externally. This condition leads me to believe that, although in some instances such stamen bundles may have been derived from single stamens by a process of multiplication of another primordia, or "dédoublement," as Leins (1964, 1971) maintains, this has not always been so. Conclusions based upon comparisons between ovules and megasporophylls, which will be presented elsewhere, have led me to believe that among known fossil forms, those most nearly related to ancestors of the angiosperms are the cupule-bearing Pteridosperms such as Caytoniales (Thomas, 1925) and Corystospermaceae (Thomas, 1933). If this hypothesis is correct, then the structure of the microsprophylls in these forms should be considered. In no case do they consist of flat structures bearing sporangia upon their surfaces, as would be expected on the basis of the "classical" concept of the origin of stamens (Eames, 1961). They are always branched, and bear numerous microsporangia at the ends of the branches. The stamen bundles in genera like *Paeonia* could be derived from such microsporangiophylls by suppression of their branches.

This discussion can be summarized by stating the hypothesis that "fusions" of stamens are of two kinds. The existence of stamen bundles that are evident chiefly from examination of the vascular pattern, and are seen with difficulty or not at all when one examines the external structure of the flower, represents a primary fusion, which takes place at the very earliest stage of androecial development, and reflects an ancestral condition. On the other hand, the staminal tube of the Malvaceae, and the elevated clusters of stamens that are found in many genera of

Hypericaceae and Myrtaceae, as well as similar structures in various other families, are secondary in origin, and are produced by intercalary meristems that appear relatively late in development, after the anther primordia are fully differentiated. This hypothesis is entirely in accord with that of conservatism of gene complexes affecting early developmental stages.

A Plea For Further Research in the Field of Morphogenetic Taxonomy

The account which I have just given of the comparative development of achenes in the Compositae reports only the beginning of a small piece of research. Nevertheless, it shows that careful comparisons between developmental patterns of selected organs in a series of closely related forms can reveal similarities and differences that are not evident from examinations of mature organs. Moreover, some of these differences in pattern can serve as a guide to evolutionary direction.

In their efforts to broaden their field, botanists have, in recent years, been relying to an increasing extent on characteristics other than external morphology. Cytotaxonomy, based upon chromosomal differences, has been with us for a long time. More recently, chemotaxonomy has increased in popularity, and is yielding highly significant results. In my opinion, the essentially undeveloped field of morphogenetic taxonomy also needs to be developed. Its potential importance lies in the prospect that it may contribute more to our understanding of morphological taxonomy than any other field. The cytotaxonomist studies chromosomes as they appear during mitosis, when the DNA is condensed into neat packages, and the genes are inactive. Innumerable studies in this field have shown us that the number and shape of these "packages" is much less important for adaptation, survival, and ecological distribution than is the nature of the genes contained in them. Chemotaxonomists, because of the complexity of their field, have been forced to concentrate upon certain compounds and properties largely because of technical considerations that determine the ease of study rather than criteria of evolutionary significance. We have, therefore, many systematic comparisons of secondary and accessory compounds such as phenolics and terpenes, as well as of a single property, electrophoretic mobility, possessed by those proteins that are easily isolated and recognized. Important as these investigations

are, they explore only the fringes of the biochemical systems of the organisms concerned.

The potential value of morphogenetic taxonomy arises from the fact that adult structures appear as a result of patterned sequences of gene action in development. Groups of genes are activated and deactivated according to a specific program that is controlled by a complex system of regulator genes (Britten and Davidson, 1969). Morphological evolution must be based ultimately upon mutations and recombinations of these particular genes. By developing the discipline of morphogenetic taxonomy, botanists may be able to approach closer to an understanding of how these genes work, and how they change during evolution.

LITERATURE CITED

BRITTEN, R. J., AND E. H. DAVIDSON. 1969. Gene regulation for higher cells: a theory. Science, 165: 349–357.

CARLQUIST, S. 1969. Toward acceptable evolutionary interpretations of floral anatomy. Phytomorphology, 19: 332–362.

CELAKOWSKY, L. 1896. Über den phylogenetischen Entwicklungsgang der Blüte. Sitzber. K. Böhm. Ges. Wiss. Math. nat. Kl., 1896: 1–91.

DARWIN, C. 1812. The Origin of Species. 6th London Edition.

DEBEER, G. R. 1951. Embryos and Ancestors, Revised Edition. Oxford University Press.

DOUGLAS, G. E. 1957. The inferior ovary. II. Bot. Rev., 23: 1–46.

EAMES, A. J. 1931. The vascular anatomy of the flower, with refutation of the theory of carpel polymorphism. Amer. J. Bot., 18: 147–188.

——————. 1961. Morphology of the Angiosperms. New York: McGraw Hill.

HEEL, W. A., VAN. 1966. Morphology of the androecium in the Malvales. Blumea, 13: 177–394. .

HERR, J. M., JR. 1971. A new clearing-squash technique for the study of ovule development in angiosperms. Amer. J. Bot., 58: 785–790.

HIEPKO, P. 1965. Das zentrifugale Androecium von Paeonia. Ber. deu. bot. Ges., 77: 427–435.

HUETHER, C. A., JR. 1968. Exposure of natural genetic variability underlying the pentamerous corolla constancy in Linanthus androsaceus ssp. androsaceus. Genetics, 60: 123–146.

KAPLAN, D. R. 1967. Floral morphology, organogenesis and interpretation of the inferior ovary in Downingia bacigalupii. Amer. J. Bot., 54: 1274–1290.

——————. 1971. On the value of comparative development in phylogenetic studies — a rejoinder. Phytomorphology, 21: 134–140.

LEINS, P. 1964. Die frühe Blütenentwicklung von *Hypericum hookerianum* Wight et Arn. und *H. aegypticum* L. Ber. deu. bot. Ges., **77**: 112-123.

————. 1971. Das Androecium der Dicotylen. Ber. deu. bot. Ges., **84**: 191-193.

MELVILLE, R. 1962. A new theory of the angiosperm flower: 1. The gynoecium. Kew Bull., **16**: 1-50.

MURBECK, S. 1914. Über die Baumechanik bei Änderungen im Zahlenverhältnis der Blüte. Lunds Univ. Arsskr., N.F., Afd. 2, **11** (3) : 1-36.

OLSON, K. C., T. W. TIBBITS, AND B. E. STRUCKMEYER. 1969. Leaf histogenesis in *Lactuca sativa* with emphasis upon laticifer ontogeny. Amer. J. Bot., **56**: 1212-1216.

PURI. V. 1951. The role of floral anatomy in the solution of morphological problems. Bot. Rev., 17: 471-553.

————. 1952. Placentation in angiosperms. Bot. Rev., **18**: 603-651.

ROBSON, N. K. B. 1972. Evolutionary recall in *Hypericum* (Guttiferae) ? Trans. bot. Soc. Edinburgh, **41**: 365-383.

STEBBINS, G. L. 1937. Critical notes on *Lactuca* and related genera. J. Bot., **75**: 12-18.

————. 1940. Studies in the Cichorieae: *Dubyaea* and *Soroseris*, endemics of the Sino-Himalayan Region. Mem. Torrey bot. Club, **19**: 1-76.

————. 1950. Variation and Evolution in Plants. New York: Columbia University Press. 643 pp.

————. 1967. Adaptive radiation and trends of evolution in higher plants. *In* Evolutionary Biology. Th. Dobzhansky, M. K. Hecht, and Wm. C. Steere, eds. Vol. 1: 101-142.

SWAMY, B. G. L. 1949. Further contributions to the anatomy of the Degeneriaceae. J. Arnold Arb., **30**: 10-38.

THOMAS, H. H. 1925. The Caytoniales. a new group of angiospermous plants from the Jurassic rocks of Yorkshire. Phil. Trans. roy. Soc. London, B, **213**: 299-313.

————. 1933. On some pteridospermous plants from the Mesozoic rocks of South Africa. Phil. Trans. roy. Soc. London, B, **222**: 193-265.

TORREY, J. G. 1955. On the determination of vascular patterns during tissue differentiation in excised pea roots. Amer. J. Bot., **42**: 183-198.

————. 1957. On the determination of vascular pattern formation in regenerating pea root meristems grown *in vitro*. Amer. J. Bot., **44**: 859-870.

WETMORE, R. H., AND J. P. RIER. 1963. Experimental induction of vascular tissues in callus of angiosperms. Amer. J. Bot., **50**: 418-429.

WILSON, C. L. 1965. The floral anatomy of the Dilleniaceae. I. *Hibbertia* Andr. Phytomorphology, **15**: 248-274.